

The tortoise and the hare: A race between native tree species and the invasive Chinese tallow

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ABSTRACT

Species-specific growth rate and its response to interspecific competition can determine the winners and losers in forest stand development following disturbance. In the southeastern US, Chinese tallow [*Triadica sebifera* (L.) Small], a non-native, fast-growing, invasive tree readily displaces native species. However, its rapid early height growth may not compensate for its shorter ultimate stature and earlier senescence when competing with fast growing native tree species of larger stature and longer lifespans. In this study, we compared the growth and competitiveness of Chinese tallow to two native species, slash pine (*Pinus elliottii* Englem.) and sweetgum (*Liquidambar styraciflua* L.), using two datasets representing different spatial scales. Plot data from Parris Island, South Carolina obtained by conducting stem analyses, were used to determine height and diameter growth patterns in relation to age and competition. Landscape-scale data from the U.S. Forest Inventory and Analysis (FIA) program were used to determine the relationship of relative importance value (rIV) and periodic annual DBH increment along a competition gradient. We found that Chinese tallow displayed faster diameter and height growth initially, but slowed down considerably after eight years, compared to slash pine. Slash pine was the least tolerant of competition among the three species, and competition had less effect on the growth of Chinese tallow and sweetgum. Our findings suggest that stand-replacing disturbance favors the rapid growth of Chinese tallow for the first decade, even under intense competition. Further, the establishment of native tree species would require effective control of Chinese tallow immediately following disturbance. Efforts to manage Chinese tallow while promoting the growth of native trees may include site preparation to reduce initial abundance of this invasive species, artificial regeneration of native species to provide them 'head-start' during the first few years of growth, and release treatments early in stand development to reduce competition for native species.

1. Introduction

Invasiveness, the capacity of a species to become established in large numbers and prolifically reproduce, is often related to rapid growth and overall larger size of the invading species, which allows it to be highly competitive in introduced environments (Pyšek and Richardson, 2007). Reports of impacts from invasive species are increasingly prominent in the literature (Richardson et al., 2014; Hirsch et al., 2017), with many invasive trees being among the most widespread and damaging of all invasive plant species (Weber, 2003; Richardson and Rejmánek, 2011). Trees have the longest lifespans among plants. Understanding long-term growth dynamics of both invasive and native tree species is critically important to measuring the success and impact of any invasive tree species in a native forest

community (D'Antonio and Flory, 2017). However, principles of stand-level developmental processes are rarely applied to study successional patterns for invasive tree species, in part, because of rarity of long-term studies.

The tendency of invasive plants to become spatially and numerically dominant in their introduced ranges may contribute to site and landscape homogenization, and thus, negatively affect biodiversity (McKinney and Lockwood, 1999). The spatial distribution and local abundance of forest trees can be attributed to a range of processes, including competitive interactions among and within species, disturbance events and regimes, as well as localized dispersal (Ipanga et al., 2008). In a competitive environment, resources can be divided proportionally to competing individuals, or asymmetrically where the fast-growing or larger individual captures a disproportionate share of

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the resources, leading to the exclusion of one species over the other (Schwinning, 1996). Both competition intensity and relative advantage change over time, with some species expressing dominance earlier (i.e., pioneer species) while others assuming dominance later (i.e., late successional species).

In the context of forest stand dynamics, competitive exclusion of tree species begins in earnest during the ‘stem exclusion’ phase of stand development (Oliver and Larson, 1996). It is during this stage of development that species growing together may compete asymmetrically due to their different growth rates, resulting in slowed growth or death of the suppressed or overtopped species. Frequently, pioneer species grow rapidly when young and dominate the growing space that would otherwise be available for other species. Over time, the early rapid height growth of one species can be offset by the sustained growth or longer life span of other species with tolerance to competition and light requirements being important factors in relative success. For example, some cherry species (*Prunus* spp.), quickly die off once overtopped by other species even though they initially dominate (Marks, 1974, Hibbs, 1983). Other species, such as quaking aspen (*Populus tremuloides* Michx.) and gray birch (*Betula populifolia* Marshall), have such short life spans that they die before becoming dominated by other species (Oliver, 1978, Wang, 2003). In eastern US forests, it has been widely reported that fast growing, non-native tree species often outcompete native species during juvenile stages (Call and Nilsen, 2003, Camarillo et al., 2015, Rebbeck et al., 2017), but few examined their long-term competitive relationships. If this juvenile stage dominance continues throughout the stand development process, the invasion could ultimately result in local extinction of native species and alter the structure, composition, and function of forested communities. Therefore, determining how invasive plants compete with native species throughout all stages of stand development may be critically important for control and management of invasive species.

Chinese tallow [*Triadica sebifera* (L.) Small] is a non-native, highly invasive tree species that is rapidly increasing in abundance and distribution in the southeastern US coastal plain (Oswalt, 2010), especially following disturbance (Johns et al., 1999, Harcombe et al., 2009, Siemann et al., 2009, Fan et al., 2012, Pile et al., 2017b, Fan, 2018). However, these trees are relatively short-lived and small in stature compared to some fast-growing native species. Chinese tallow trees can live up to 100 years, but they can become senescent at < 50 years old and typically reach heights of only 7–11 m (Pile et al. 2017c). In comparison, co-occurring native slash pine (*Pinus elliottii* Englem.) and sweetgum trees (*Liquidambar styraciflua* L.) can live for centuries and reach heights of 30 m or greater (Kirkman et al., 2007). Sweetgum has strong excurrent growth and managed as a native invasive in some parts of its range due to its ability to monopolize the reproduction pool following disturbance (Kormanick, 1990). Slash pine is one of the fastest growing southern yellow pines and grown for commercial production (Lohrey and Kossuth, 1990). Due to its rapid early growth, slash pine is known to replace longleaf pine in the absence of fire (Pile et al., 2017a). The ranges of slash pine, sweetgum, and Chinese tallow overlap across the southeastern US coastal plain where all are considered fast-growing and capable of dominating sites following disturbance (Kormanick, 1990, Lohrey and Kossuth, 1990, Gan et al., 2009, Camarillo et al., 2015).

We selected to compare the growth and competitiveness of Chinese tallow to slash pine and sweetgum because they are also fast-growing species, occur in the invaded range of Chinese tallow, and in the case of sweetgum, is also broadleaved and deciduous. The objectives of this study were to (1) characterize the growth of the invasive Chinese tallow in relation to slash pine and sweetgum, two native, fast growing and longer-lived species; (2) determine competitive dynamics among these three species throughout early stand development as it relates to tree size; and (3) determine the relative effects of competition on the three species. Our specific hypotheses were: (1) because of the high comparative growth rates typically associated with invasiveness, Chinese

tallow will out-perform both native species in early stages of stand growth; (2) due to slash pine and sweetgum being longer lived and larger statured, the two native species will eventually overtop Chinese tallow as time since disturbance progresses; and (3) of the three species, Chinese tallow would be the most tolerant of competition from its neighbors due to its ability to survive, grow, and reproduce in both shaded and high-light environments (Jones and McLeod, 1990, Lin et al., 2004, Paudel and Battaglia, 2015). To test these hypotheses, we used two sources of data: (1) site-level data consisting of direct measurements of growth rate following disturbance using stem analysis, and (2) landscape-level data collected from Forest Inventory and Analysis (FIA).

2. Methods

2.1. Site data

To determine growth characteristics of the three species, we selected three study sites at Parris Island Marine Corp Recruit Depot (referred to as “Parris Island” hereafter). Parris Island is located in Beaufort County, SC (Lat. 32.3289 N, Long. –80.6947 W) and resides in the Southern Coastal Plain eco-region (EPA, 2013) (Fig. 1). Chinese tallow has been present on Parris Island since at least the 1960s and has experienced an exponential increase in abundance (Pile et al., 2017b).

In May 2012, we located the three sites at Parris Island that met our specifications with known harvest years in 1998 (stand A), 2003 (stand B), and 2008 (stand C). Sites selected were landings used as part of timber harvests (i.e., thinning of slash pine plantations) with few post-harvest residual trees, representing initial starting points (stand-replacing disturbance event) for competition following disturbance. Each landing was approximately 0.5–1.2 ha in size. The three sites are similarly protected from the influence coastal stressors (e.g., wind, salt spray) and were located within 2 km of each other. Selection of subject trees were based on the following criteria: (1) dominant or co-dominant Chinese tallow with priority for dominant trees; (2) each Chinese tallow was assessed for a near competitor (i.e., within 2 m of the subject Chinese tallow and with near-touching crowns of a similar class) of either slash pine or sweetgum (Fig. 2). Selected individuals of all three species were of natural origin and efforts were taken to select individuals of seed origin (i.e., no basal crook and single stemmed). However, parent trees of slash pine may include improved varieties that were established as pine plantations on Parris Island during the 1960s and 1970s. Chinese tallow and slash pine were collected on all three sites, but sweetgum was only collected on one site, which subsequently limited our findings for this species at Parris Island. For each individual, species, height, and crown position was recorded. In addition, the nearest three competitors were recorded for distance from subject tree and DBH (cm). However, both Chinese tallow and sweetgum are known root sprouters, and observations of sprout origin stems comprising 70% of sweetgum individuals in plots have been reported (Kormanick, 1990).

We destructively sampled 106 trees across the three sites, 16 were sweetgum, 41 were slash pine, and 49 were Chinese tallow. Tree cross-sections for stem analysis were taken at heights of 0 (ground line), 30 cm, 60 cm, 90 cm, and thereafter 50 cm intervals to the top of the tree (Fig. 2). Surfaces of stem disks were smoothed with progressively finer grades of sand paper using an orbital sander until cellular detail of rings was revealed. Diameter (mm) was recorded for each disk using a digital caliper by measuring the distance across the disk at a random starting point, and then two additional measurements were taken at 45 degrees. We averaged those three measurements to estimate diameter of each cross-section for every stem.

Annual ring boundary determination on cross-sections was assessed under 10–40× magnification for each species. Chinese tallow wood has a semi-ring porous structure and ring differentiation was determined by an decrease in cell size that often corresponded to decreases in radial

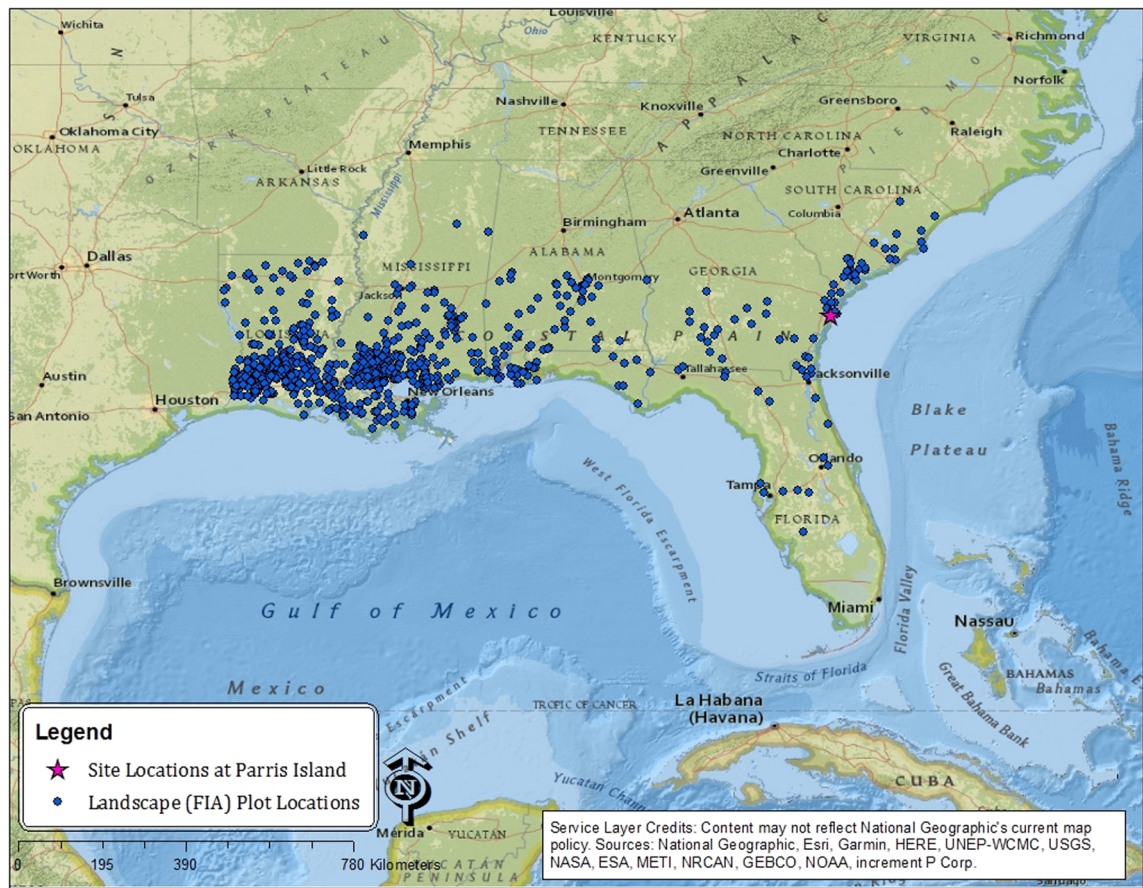


Fig. 1. Map of the 712 landscape (Southern Research Station – Forest Inventory & Analysis) plot locations and the location of the sites on Parris Island in South Carolina.

pore clusters from earlywood to latewood (giving a visual appearance of snowmen under magnification). For each tree, annual ring boundaries were demarcated on each disk and number of annual rings recorded. To determine annual diameter growth increment, we selected the disk taken at 30 cm above-ground to measure ring width using a Velmex Tree Ring Measuring System (Velmex, Inc. Bloomfield, NY). We

used patterns in annual diameter growth data to establish a baseline measurement to compare across individuals at each of the three sites. This baseline was used to compare annual growth years amongst and between species to reduce the chances of incorrectly interpreting false rings.



Fig. 2. Picture depicting site collected data for co-occurring Chinese tallow, slash pine, and sweetgum. Trees were selected together (pairs or triplets), representing near competitors, from similar crown classes.

2.2. Landscape data

Forest Inventory and Analysis (FIA) data across six southern US states where slash pine commonly occurs (AL, FL, GA, LA, MS, and SC) were used to analyze patterns of growth and competition among the three species. Forest Inventory and Analysis collects consistent inventory data on sample plots located randomly within a systematic national grid of cells, each roughly 2428 ha in area (Bechtold and Patterson, 2005). The inventory of trees at least 12.7 cm DBH occurs on FIA's standard "Phase 2" (P2) plot-cluster of four 7.3 m fixed-radius subplots, while seedling and sapling (2.5–12.7 cm DBH) inventories occur on a 2.1 m microplot within each subplot (Bechtold and Patterson, 2005).

All FIA data were acquired from the online database portal (<https://apps.fs.usda.gov/fia/datamart>). We included all publicly available inventory years since 1999 at the time of download (24 October 2017). We limited analyses to plot locations with a Chinese tallow presence recorded at some point during the study period, which resulted in 1407 plot records at 712 plot locations (Fig. 1). The three study species had similar rates of occurrence along the gradient of the site productivity classes reported for each plot in the FIA data (Fig. 3).

The majority of plot locations were visited $\leq$ twice (85%) during the study period, though some were visited up to four times. Only live trees were used in analyses. For regional demographic data, we calculated species importance values (IV) by averaging three relative measures (frequency, density, basal area) across subplots. We then calculated a relative importance value (rIV) for each species on a plot-cluster.

2.3. Data analysis

2.3.1. Height and diameter growth following disturbance

We determined tree growth since the last stand-initiating disturbance using regression models fitted separately to height and diameter growth by species from stem analysis. For height growth (cm), we used tree age determined at each cross-sectional height and related height to time since disturbance (years) for each sample tree by species and site. For diameter radial growth (mm), we used diameter incremental growth measured at the 30 cm cross-section where annual diameter growth was measured and related radial diameter growth to time since disturbance (years) for each sample tree by species and site. The best-fitting linear models and non-linear models for each species were selected using multiple statistical criteria including cross-validation and R^2 for both height and radial diameter growth. Incremental growth for height and diameter was defined as the mean annual growth over the study period.

To test the hypothesis that Chinese tallow will outcompete slash pine and sweetgum by overall tree size, we used ANOVAs to compare height by time since disturbance and regression techniques to estimate relationships between total tree height and tree age (HGT/age), tree DBH and tree age (DBH/age), and height by DBH (HGT/DBH) for each species.

2.3.2. Competition tolerance

To assess our third hypothesis, regarding the effect of competition on early tree growth, we used site data to quantify the relationship between competition index and tree size (HGT and DBH) using

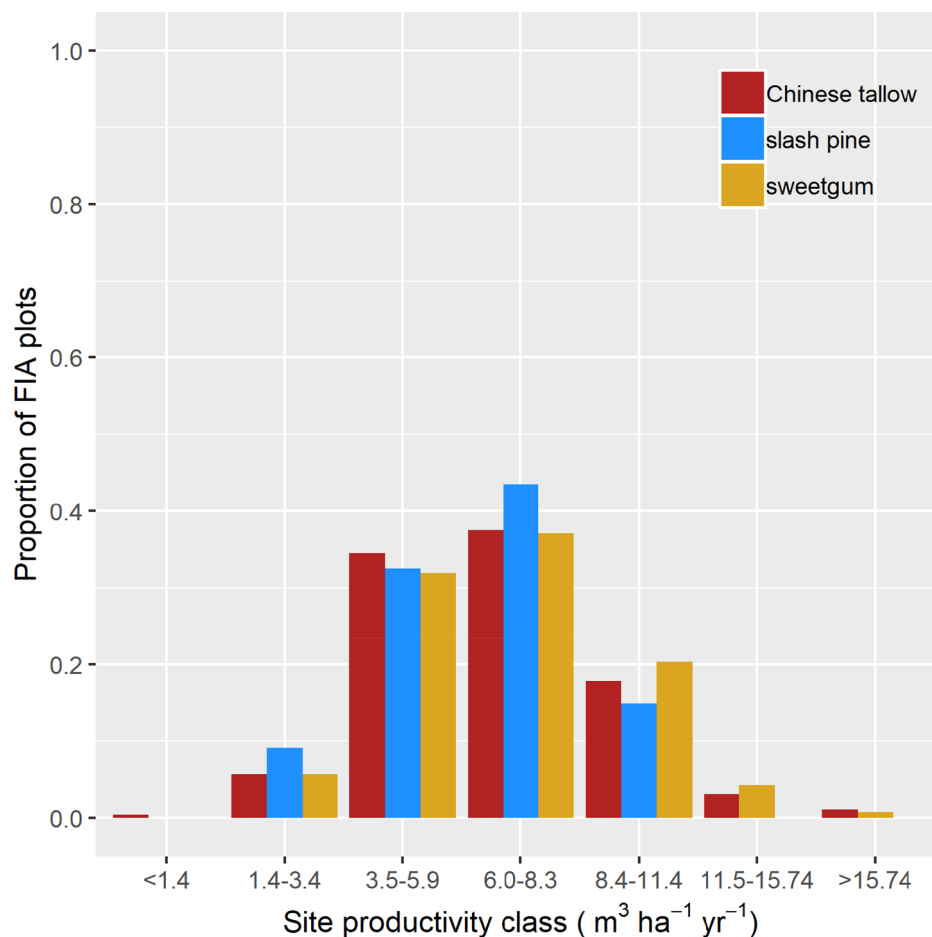


Fig. 3. Distribution of landscape data plots across the study region by site productivity class (as classified by FIA) for each study species.

regression analysis and compared the relationship among species. The competition index used in the study was calculated across all sites and species based on a distance weighted ratio of the four nearest competitors to each subject tree (Daniels, 1976).

$$CI_i = \sum_{j=1}^n (D_j/D_i)/DIST_{ij}$$

where CI_i is the competition index of the subject tree (i), D is the DBH, $DIST_{ij}$ is the distance between tree i and competitor j , and N is the number of competitors. This type distance weighted measure accounts for stand developmental processes as DBH size and distance to competitors (i.e., smaller DBH and short-distances during early growth and larger DBH and longer-distances as the stand ages and natural thinning occurs) are a function a competitive even-aged environment. As a result, a high competition index at any stand age would result in a reduction in survivorship, growth, and reproduction of competing individuals (Begon et al., 1996).

We also assessed competition at the landscape level using FIA data. Mixed-effects linear regression (Pinheiro and Bates, 2000) was used to model the response variable, mean periodic annual DBH increment (PAI_D), as a function of species, the total basal area of larger trees (BAL_{SUB}) on a subplot, and their interaction as fixed-effects. BAL is a commonly used one-sided competition index (Weiskittel et al., 2011). Because the FIA sampling design measures sapling size trees on microplots only, the previously defined two-sided competition index could not be fully calculated outside the microplot. Random-effects (intercept-only) included the individual plot locations (due to the possibility of > 2 visits), plot-cluster within location, and subplot within plot-cluster. Preliminary analyses found that transforming the response variable by adding a constant (1) and taking the natural log improved model diagnostics. We assumed negative PAI_D values in the data were likely due to measurement errors and excluded those trees from further analyses.

In addition to mean PAI_D , near-max PAI_D (90th percentile) was modeled via quantile regression using the previously described fixed-effects to further isolate the effect of a single growth limiting factor (competition in this case) when multiple limiting factors are present (Cade et al., 1999, Cade and Guo, 2000, Sun et al., 2017). Because applied tools for mixed-effects quantile regression are limited, this analysis did not incorporate the previously described random-effects.

In these landscape analyses, a statistically significant interaction term would indicate that the species differ in their ability to tolerate increasing competition. A lower slope value for Chinese tallow would indicate a slower reduction in growth with increasing competition and would provide critical support for the hypothesis that this species is highly tolerant to competition. However, differences in tolerance may be of limited ecological consequence if the magnitude of growth is considerably different among the species. Thus, when growth estimates for each species are plotted against a gradient of competition intensity, a crossing pattern among species growth estimates within commonly observed levels of BAL_{SUB} would provide evidence that the statistical differences likely have ecological significance.

Site analyses were conducted using SAS 9.3.1 and landscape analyses used R version 3.4.4 statistical software (R Core Team, 2018). Significance was determined at an alpha of $p = 0.05$. Transformed data are presented in their original values.

3. Results

Trees at Parris Island were not statistically different in cohort age between species for Stand A ($p = 0.09$) nor Stand B ($p = 0.37$; Table 1). However, in Stand C, sweetgum was slightly older than Chinese tallow ($p = 0.03$). Tree DBH at Parris Island was similar among species for each stand (Stand A: $p = 0.25$; Stand B: $p = 0.94$; and Stand C: $p = 0.24$). However, Chinese tallow was tallest among the species in

the youngest stand (Stand C: $p = 0.02$) with no differences among species as stand age progressed (Stand A: $p = 0.17$ and Stand B: $p = 0.94$). Based on the FIA data, mean stand age across the landscape was approximately 34 years (Table 2).

Based on the site data from Parris Island, Chinese tallow had the fastest initial height and diameter growth among the three study species. A power model (two parameter rise to max) was determined as the best-fitting model of height growth for Chinese tallow [$HGT = 1686.0 * (1 - 0.92^{years})$; $F = 1836.7$; $p < 0.01$; non-linear $R^2 = 0.73$] and slash pine [$HGT = 4119.5 * (1 - 0.97^{years})$; $F = 1819.9$; $p < 0.01$; non-linear $R^2 = 0.75$] (Fig. 4), which was similar to findings by Tian et al. (2017) for Chinese tallow in Mississippi. We further compared linear height growth between the three sites for slash pine and Chinese tallow to determine if differences were related to site differences or time since disturbance. For slash pine, there were no significant differences among the three sites for height growth (Supplemental Material). However, for Chinese tallow, with increasing site age there was a significant decline height growth. Due to limited sample size for sweetgum, a linear regression for time since disturbance and height was the best approximation [$HGT = 13.9 + 74.5(years)$; $F = 230.34$; $p < 0.01$; $R^2 = 0.75$].

A second-order quadratic model was the best-fitting model of radial diameter (square root transformed) for Chinese tallow [$\sqrt{diameter} = 2.2 + (0.55 * years) - (0.02 * years^2)$; $F = 334.5$; $p < 0.01$; $R^2 = 0.62$] and slash pine [$\sqrt{diameter} = 1.65 + (0.55 * years) - (0.01 * years^2)$; $F = 232.9$; $p < 0.01$; $R^2 = 0.56$] (Fig. 5). Due to limited sample size, a log-linear regression best approximated the relationship of years since disturbance and radial diameter for sweetgum [$\ln(diameter) = 1.83 + 0.67 * \ln(years)$; $F = 28.7$; $p < 0.01$; $R^2 = 0.33$].

Within sites, overall tree size depended on tree age. In initial growth stages, Chinese tallow was taller than slash pine, however as the trees aged, size metrics and dominance are indicative of slash pine's larger stature.

Initially following disturbance, mean stem height was statistically greater for Chinese tallow (Fig. 6). As trees aged, predicted total height was greater for Chinese tallow until 12 years old [Chinese tallow: $HGT = 265.78 * age^{0.55}$; $p < 0.01$; $R^2 = 0.65$. slash pine: $HGT = 126.95 * age^{0.85}$; $p < 0.01$; $R^2 = 0.76$] (Fig. 7).

For the first 6 years following disturbance, Chinese tallow height was greater than slash pine. However, mean slash pine height caught up with Chinese tallow after 6 years of age, and continued to increase (Fig. 6). After 12 years, slash pine was predicted to be taller than Chinese tallow (Figs. 6 and 7). Slash pine DBH was predicted to be larger than Chinese tallow across all ages [Chinese tallow: $DBH = 129.06(1 - (-0.07^{*age}))$; $p < 0.01$; $R^2 = 0.53$. Slash pine: $DBH = 125.45(1 - (-0.08^{*age}))$; $p < 0.01$; $R^2 = 0.45$]. Tree height for Chinese tallow began to reach a maximum at DBH around 9 cm whereas slash pine height continued to increase with increasing DBH [Chinese tallow: $HGT = 1514.16(1 - (-0.02^{*DBH}))$; $p < 0.01$; $R^2 = 0.85$; slash pine: $HGT = 2023.74(1 - (-0.01^{*DBH}))$; $p < 0.01$; $R^2 = 0.76$] (Fig. 7).

From the FIA plots with Chinese tallow present, across the landscape where interspecific competition occurred among the three species, the metrics of tree size (i.e., BA and DBH) and dominance favored slash pine over Chinese tallow and sweetgum. Slash pine had greater basal area and relative importance values than Chinese tallow or sweetgum (Table 2). Densities were similar for slash pine and Chinese tallow, and lowest for sweetgum. Slash pine had a greater number of trees per hectare in larger DBH and height classes across the landscape (Fig. 8), especially for trees over 15 cm DBH and 15 m tall. Contrarily, the height distribution of trees peaked similarly for sweetgum and Chinese tallow at 5 m with few trees greater than 15 m. However, sweetgum had trees over 24 m tall and there were few Chinese tallow above 15 m.

Generally, at both the site and landscape scale, increasing levels of competition had a negative effect on the growth of slash pine but had

Table 1

Mean (SE) tree age (years), DBH (cm), and height (m) for the field collected dominant and co-dominant Chinese tallow, slash pine, and sweetgum trees across three forest stands. Different superscript letter indicates a significant ($p = 0.05$) difference among species in a single stand.

Species	Stand A (oldest)			Stand B			Stand C (youngest)		
	Age	DBH	Height	Age	DBH	Height	Age	DBH	Height
Chinese tallow	14.5 (2.7)	8.3 (1.9)	11.7 (1.9)	10.0 (1.1)	7.2 (3.0)	9.7 (2.0)	5.3 (0.6) ^b	4.1 (2.0)	6.7 (1.8) ^a
Slash Pine	15.3 (1.1)	9.6 (3.3)	13.2 (3.2)	9.2 (1.1)	8.9 (3.4)	9.6 (1.9)	5.6 (0.9) ^{ab}	4.6 (2.6)	5.4 (1.3) ^b
Sweetgum	–	–	–	–	–	–	6.1 (0.7) ^a	3.3 (0.5)	5.5 (0.8) ^b

Harvest years: Stand A – 1998, Stand B – 2003, and Stand C – 2008.

Table 2

Demography metrics [mean (± SE)] from Forest Inventory and Analysis data (FIA).

Species	n ^a	Stand Age Yr	Density ^b			Stature ^c			Structure ^d	
			m ² ·ha ⁻¹	trees·ha ⁻¹	rIV %	QMD (cm)	HGT ^e (m)	HGT/D ^e	rHGT ^e	rD
Chinese tallow	1046		3.2 (0.15)	566 (28)	23.0 (0.7)	11.8 (0.2)	11.1 (0.1)	1.0 (0.01)	0.8 (0.01)	0.8 (0.01)
Slash pine	154		9.6 (0.75)	584 (84)	36.4 (2.2)	22.3 (0.9)	16.7 [0.5]	0.8 (0.01)	1.2 (0.03)	1.3 (0.03)
Sweetgum	772		3.6 (0.13)	393 (21)	18.4 (0.4)	16.6 (0.4)	14.1 (0.2)	1.0 (0.01)	1.0 (0.01)	0.9 (0.02)
All	1268	33.7 (0.6)	21.5 (0.3)	1907 (41)	23.6 (0.5)	14.1 (0.2)	13.7 (0.1)	0.9 (0.01)	1.0 (0.01)	1.0 (0.01)

^a n refers to the number of plot-clusters a species of interest was recorded.

^b Density is expressed as basal area and trees per hectare and the relative importance values (rIV) for the three subject species.

^c Quadratic mean diameter (QMD) refers to the average plot-cluster quadratic mean diameter. Height (HGT) refers to the average plot-cluster height. The ratio of height to diameter (HGT/D) refers to the average plot-cluster ratio of height to DBH.

^d Ratio of species height to plot height (rHGT) refers to the average plot-cluster ratio of species height to plot-cluster average height. Ratio of species DBH to plot DBH (rD) refers to the average plot-cluster ratio of species DBH to plot-cluster average DBH.

^e Note: Heights were not measured on all plot-clusters and rarely for those < 13 cm DBH.

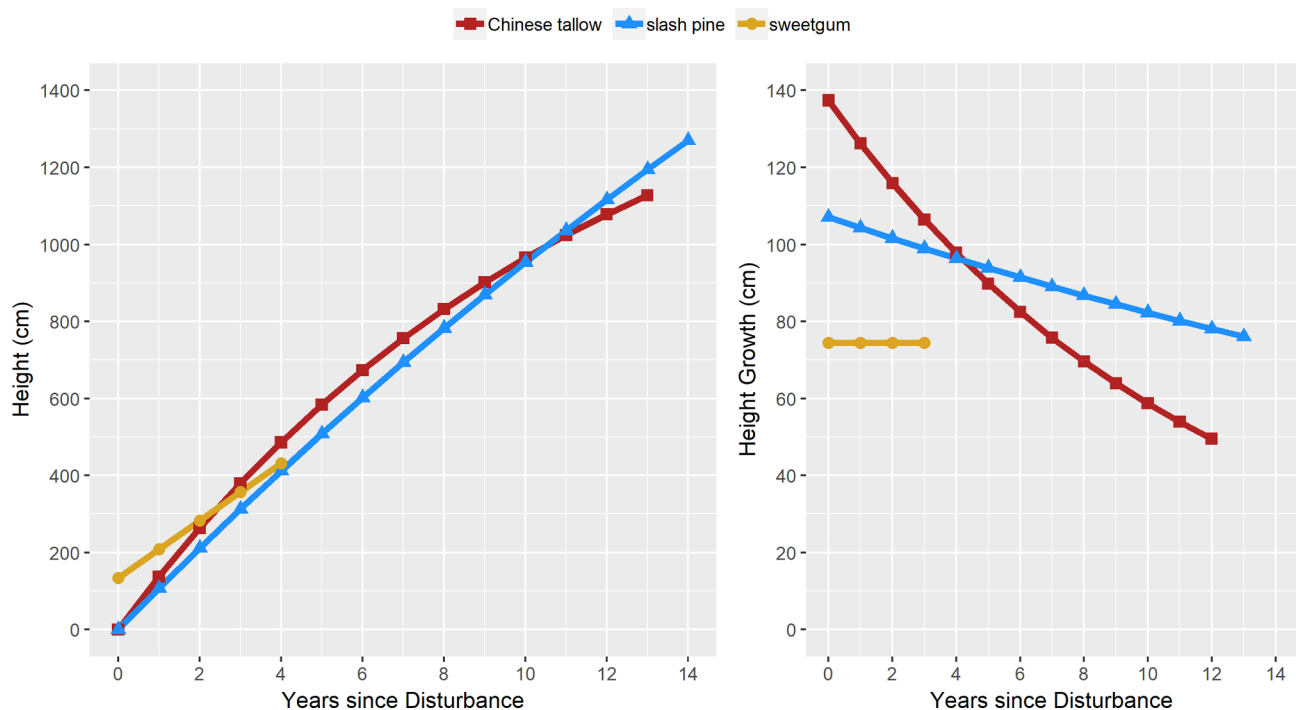


Fig. 4. Height (cm) and annual height incremental growth following disturbance for Chinese tallow, slash pine, and sweetgum across three sites at Parris Island, South Carolina.

less influence on Chinese tallow. The effect of competition on tree growth indicate Chinese tallow's capacity to maintain dominance (i.e., tree vigor and site-level abundance) even with high levels of competition. Results at the site level indicate that the effect of competition on tree DBH and height was significant for Chinese tallow and slash pine (Fig. 9; Supplemental Material). However, Chinese tallow was less sensitive to competition for both height [$HGT = 12.52^{(-0.101 \cdot CI)}$; $p < 0.01$; $R^2 = 0.27$] and DBH [$DBH = 12.03^{(-0.234 \cdot CI)}$; $p < 0.01$;

$R^2 = 0.51$] than slash pine [$HGT = 15.36^{(-0.194 \cdot CI)}$; $p < 0.01$; $R^2 = 0.30$ and $DBH = 16.22^{(-0.295 \cdot CI)}$; $p < 0.01$; $R^2 = 0.41$]. At low levels of competition, slash pine had greater height and DBH than Chinese tallow. However, at higher levels of competition, Chinese tallow had greater height and DBH than slash pine. With the limited dataset for sweetgum, tree height [$HGT = 6.67-0.38(CI)$; $p < 0.01$; $R^2 = 0.42$] and DBH [$DBH = 4.4-0.31(CI)$; $p < 0.01$; $R^2 = 0.43$] followed a linear pattern in response to competition.

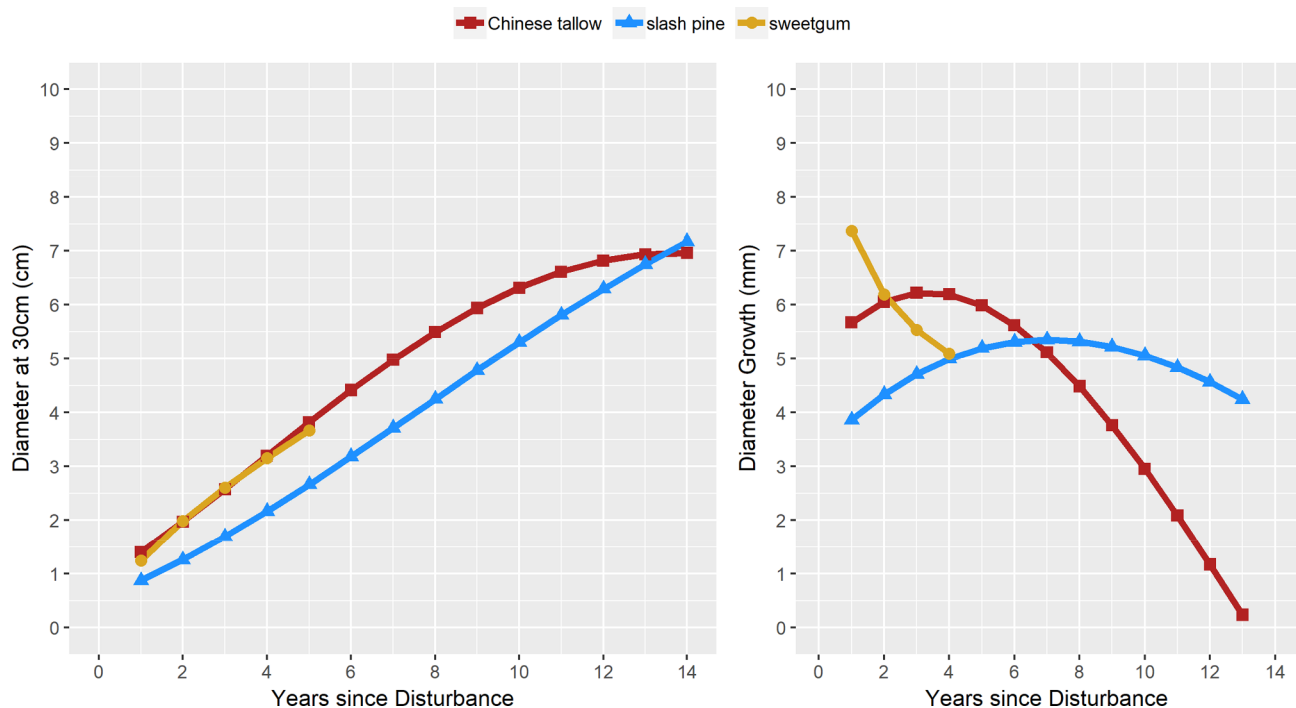


Fig. 5. Radial diameter (cm) and annual diameter incremental growth determined at 30 cm above ground-line following disturbance for Chinese tallow, slash pine, and sweetgum across three sites at Parris Island, South Carolina.

Similarly, at the landscape level, the Species * Competition interaction term was statistically significant for both mean PAI_D ($p < 0.01$) and near-max PAI_D ($p < 0.01$) indicating that the species differed in their tolerance to increasing competition (Fig. 10, left panel). The slope of both mean and near-max PAI_D illustrate the decline in growth with increased competition. The slopes of all three species were statistically different following slash pine (least tolerant) > Chinese tallow > sweetgum (most tolerant). While the rate of decline in mean PAI_D was statistically different between Chinese tallow and sweetgum, the estimates largely overlapped across much of the range of competition examined, suggesting those mean differences may have limited biological consequence. The plotted estimates of mean PAI_D show that slash pine had greater growth than all other species at low levels of competition but a sharper decline with increasing basal area in larger trees. Once BAL_{SUB} reached $25\text{--}30\text{ m}^2\text{ ha}^{-1}$ the growth of both Chinese tallow and

sweetgum matched slash pine and began to outpace it thereafter. The potential ecological consequences of the limiting effects of increasing competition on growth were more notable in the plotted estimates of near-max PAI_D (Fig. 10, right panel). While slash pine showed a growth advantage at low levels of competition, similar to mean PAI_D that advantage was lost with increasing competition much sooner. The growth of Chinese tallow with competition matched slash pine once BAL_{SUB} reached about $15\text{ m}^2\text{ ha}^{-1}$ and considerably outpaced slash pine with increasing levels of competition beyond about $20\text{ m}^2\text{ ha}^{-1}$. Likewise, sweetgum matched and increasingly exceeded slash pine growth once BAL_{SUB} reached about $20\text{ m}^2\text{ ha}^{-1}$ and beyond. Chinese tallow was able to maintain a slight growth advantage over sweetgum across much of the range of competition analyzed, but their growth rates became indistinguishable beyond about $30\text{ m}^2\text{ ha}^{-1}$.

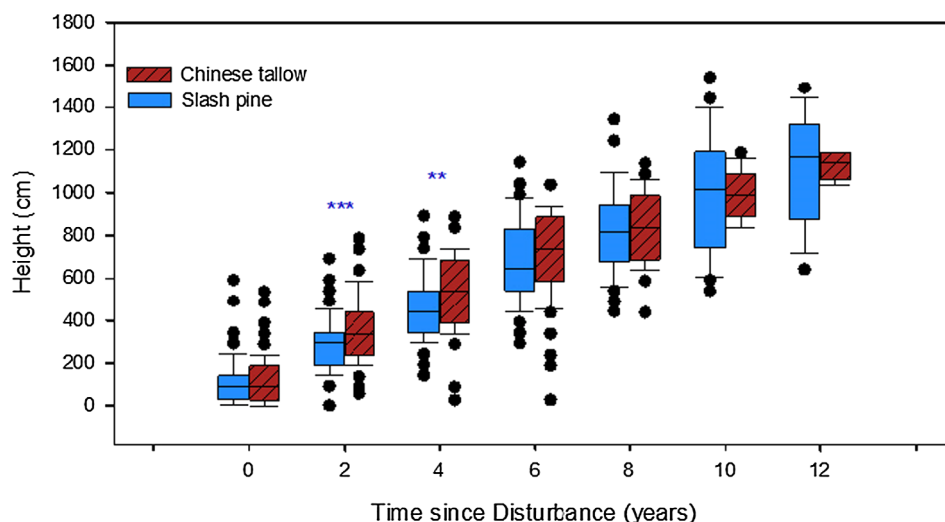


Fig. 6. Comparison of tree height among years (2 year classes) since disturbance (level of significance: $p < 0.01 = **$ and $p < 0.001 = ***$). Box plot represents the interquartile range. Whiskers represent 10th and 90th percentiles with all outliers indicated as points outside of the whiskers.

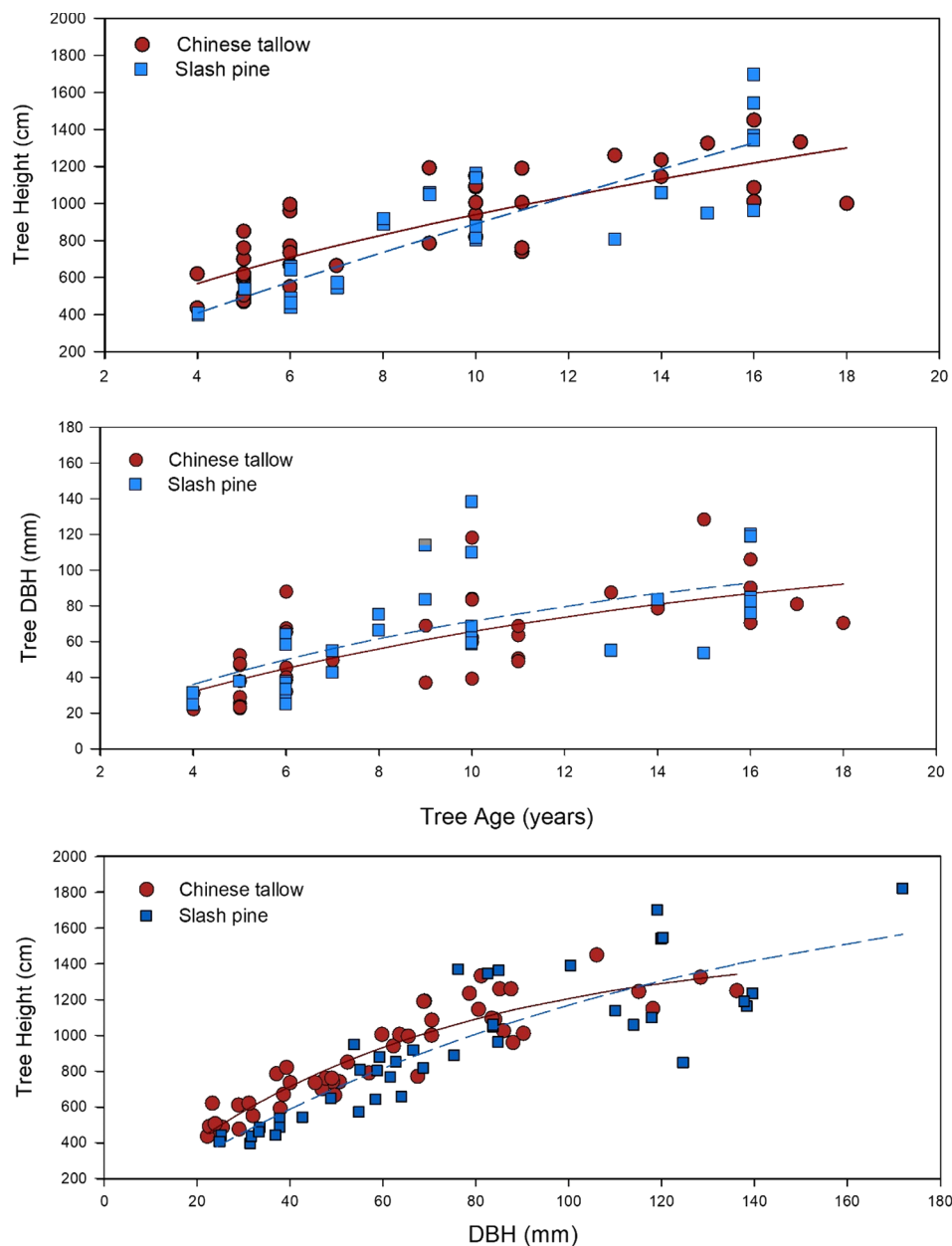


Fig. 7. Relationship of actual Chinese tallow (red solid line) and slash pine (blue dashed line) tree age to total tree height (cm) and tree DBH (mm), as well as the relationship of tree DBH to total tree height at Parris Island, South Carolina. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Trees are long-lived organisms, and their growth trajectories differ greatly among species. To our knowledge, most studies on the growth of Chinese tallow are either through short-term, manipulative studies (Scheld and Cowles, 1981) or from biometric models that do not account for competition for growing space, especially with native fast growing tree species (Pile et al., 2017c, Tian et al., 2017). Few studied long-term growth dynamics of and competitive interactions between Chinese tallow and native tree species, which is critical to developing strategies for local and regional control of invasive trees. In this study, we sought to determine the growth of Chinese tallow in natural stands in relation to native species. We used two types of information: (1) direct measurements from site data comparing growth of Chinese tallow to two native species (slash pine and sweetgum) in early stand development; and (2) landscape data from across the overlapping range

of the three species in the southeastern US across a wide range of age classes and stand development. By using site and landscape data, we were able to explore species interactions at two spatial scales that are relevant to management. We found that Chinese tallow had faster rates of growth when young and was more tolerant to competition at both the stand and landscape scale, but these advantages diminished over time, with fast growing native tree species such as slash pine being able to catch up in growth in about 12 years. These results indicate that Chinese tallow may be outcompeted in height growth over the long-term when in lower densities. However, in high Chinese tallow densities, there is a need to suppress Chinese tallow invasion while promoting the establishment of fast growing native tree species during stand initiation stage. Such suppressive actions should aim to prevent the dominance of Chinese tallow in a forest canopy and maintain the long-term integrity of native forest communities.

As expected, our study confirms that Chinese tallow exhibits fast

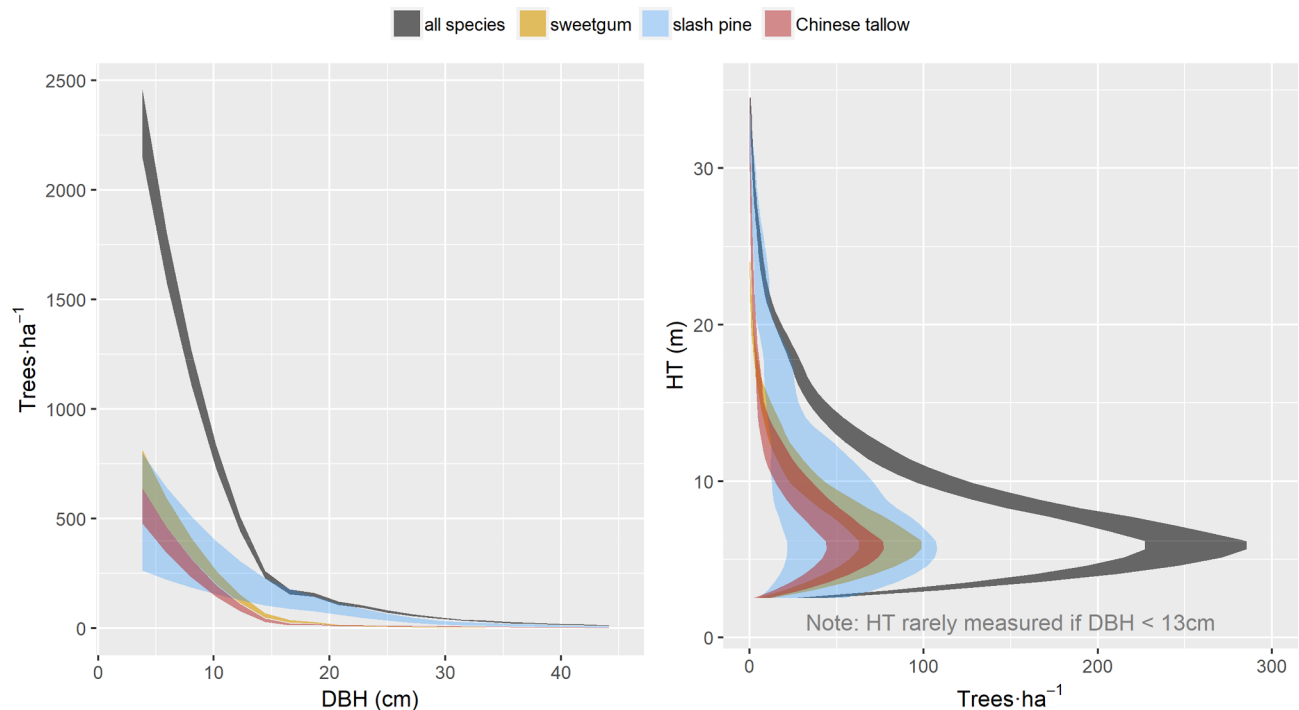


Fig. 8. Distribution of trees per hectare by diameter at breast height (DBH, cm) and height (m) for Chinese tallow, sweetgum, slash pine and of all species recorded in 1407 FIA plot records from 6 southern US states. Species ribbon width represents 95% confidence interval of the mean.

rates of growth for the first few years following disturbance. Scheld and Cowles (1981) reported Chinese tallow grew up to 2.8 m tall two years following germination, and up to 5.5 m after two years following coping. Our results were similar, approximating 3.1 m tall two years following a stand-replacing disturbance. However, sweetgum initial height growth can be variable depending on site conditions (Kormanick, 1990). Because of the limitations with our dataset for sweetgum, we could only determine sweetgum growth rates for four years following disturbance on one site, which indicated that mean sweetgum height was approximately 2.8 m two years after disturbance. Initial growth of slash pine may be slower than that of either sweetgum or Chinese tallow, with slash pine's first year height of 0.9 m under optimal greenhouse conditions (Pile et al. 2017a). At Parris Island, slash pine was 2.6 m in height and shorter than either Chinese tallow or sweetgum two years following disturbance. Given this early height growth advantage, Chinese tallow would likely overtop the two fast growing native tree species. In areas with established Chinese tallow, release treatments that suppress the competition from Chinese tallow become necessary to promote the early establishment of native tree species.

As age since disturbance progressed, Chinese tallow's initial height growth diminished in comparison to slash pine. Specifically, slash pine height and diameter growth rate exceeded that of Chinese tallow at the mean ages of 5 and 8 years, respectively and slash pine height surpassed Chinese tallow at 12 years old. Although limited to make conclusions regarding the growth and competitive dynamics of sweetgum from our site data, from the landscape data, sweetgum was reported in larger height and diameter classes in comparison to Chinese tallow. The tallest Chinese tallow from our site data was approximately 14 m, and the majority of the population across the landscape, as indicated by the FIA data, were well under 15 m tall. In contrast, both sweetgum and slash pine have strong excurrent growth and can reach heights of 30 m at maturity, with slash pine capable of reaching 19.6 m in 20 years (Shoulders and Tiarks, 1980). Our results suggest that the two native species examined in this study could likely maintain their long-term dominance if not competitively excluded during early stem exclusion.

In regards to competition, some invasive species may reflect a

“Jack-of-all-trades” scenario where they are able to maintain fitness even under stressful conditions because of their greater plasticity associated with underlying morphological or physiological traits (Richards et al., 2006). Our results, from both the site and landscape data, indicate that Chinese tallow is similar to sweetgum, but more tolerant to competition than slash pine. With increasing competition, slash pine size was severely limited, but Chinese tallow and sweetgum displayed a relatively stable growth rate across the competition gradient. Although, both slash pine and sweetgum are classified as intolerant to shade, sweetgum is considered one of the most adaptable hardwood species and an exceptional competitor with its tolerance to different soil and site conditions (Kormanick, 1990) and is often managed as an undesirable species in its native ecosystems. Additionally, sweetgum is tolerant to intraspecific competition when young (Kormanick, 1990), which is likely attributed to its aggressive sprouting. Even with shading, aboveground growth of sweetgum is often unaffected under a pine overstory (Bormann, 1953, Holbrook and Putz, 1989). However, sweetgum may be sensitive to belowground competition, especially with Japanese honeysuckle (*Lonicera japonica* Thunb.) (Dillenburg et al., 1993). Chinese tallow appears to defy shade tolerance classification, but is most often considered mid-tolerant to intolerant to competition from shading (Pile et al., 2017c). Research has suggested high levels of plasticity in Chinese tallow in response to shade and water (Zou et al., 2009). Further, increased plasticity to shade following introduction has been attributed to invasion success (Zou et al., 2009, Chen et al., 2013). Therefore, the early aggressive growth of Chinese tallow will likely suppress native tree species, and intervention with from silviculture treatments early in stand development may become necessary to facilitate the establishment and growth of native tree species on the sites invaded by Chinese tallow.

5. Management implications

Although direct control (e.g., herbicides) of woody invasive species may be most effective in the short-term, allowing for natural succession may be equally effective in the long-term (Cunard and Lee, 2009). Indeed, allowing stands to develop has been suggested as an opportunity

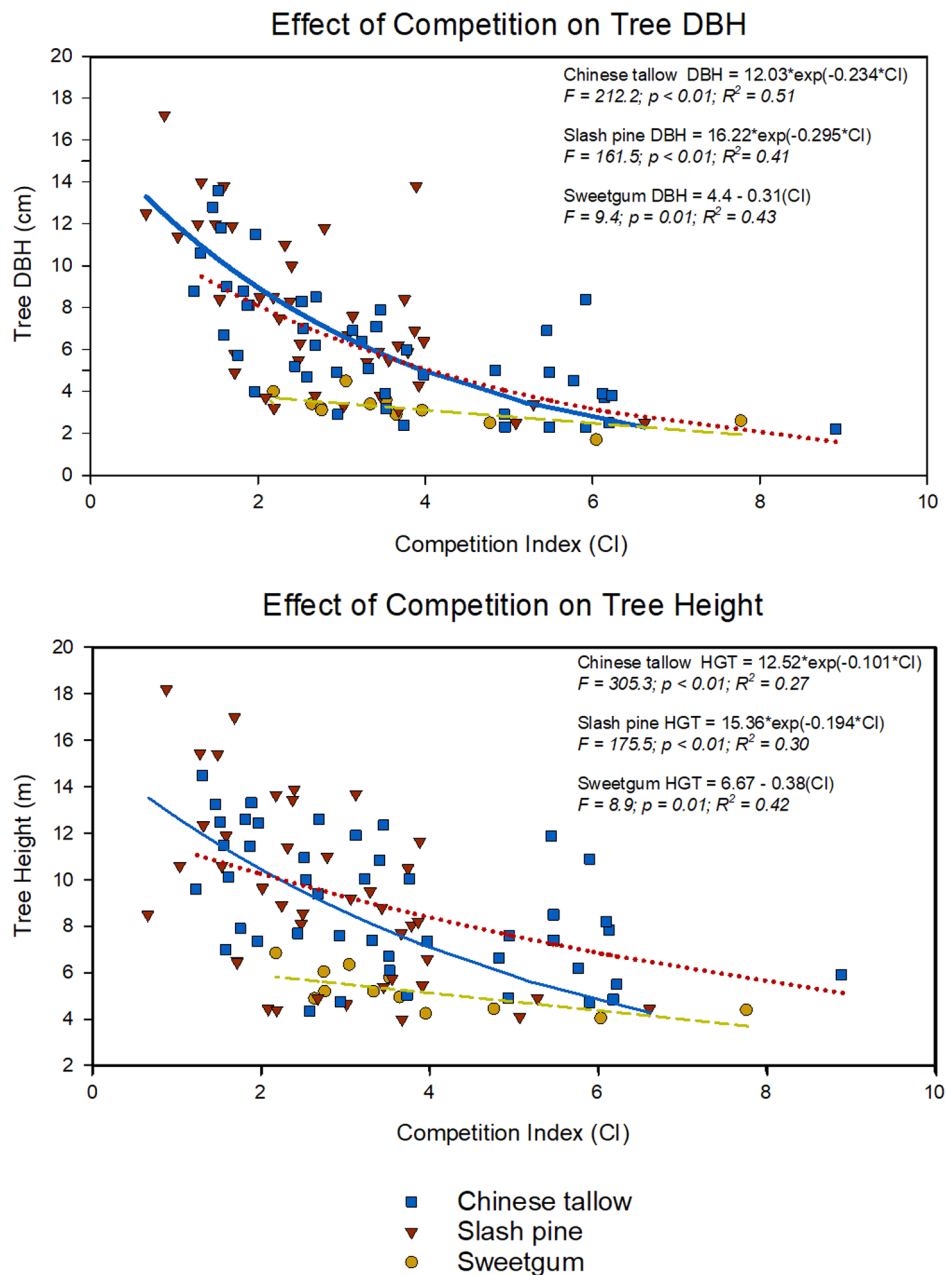


Fig. 9. The effect of competition on tree DBH (cm) and tree height (m) for Chinese tallow (fitted equation: blue solid line), slash pine (fitted equation: red short-dashed line), and sweetgum (fitted equation: yellow long-dashed line) at Parris Island, South Carolina. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to allow resource-demanding non-native species to be excluded by native late successional, resource-efficient species (Von Holle and Motzkin, 2007). Natural reforestation has also been suggested as a viable approach to limiting invasions (Rejmánek et al., 1989, Meiners et al., 2002, Simberloff et al., 2002, Von Holle and Motzkin, 2007).

Because of its faster early growth and more tolerance to competition, abundant Chinese tallow will likely suppress the regeneration of other native tree species, including fast growing species such as slash pine and sweetgum. Once established, however, fast growing native trees such as slash pine could overtop Chinese tallow in about 10–12 years and assume canopy dominance. This dynamic interaction between native and invasive tree species suggests a new alternative approach to manage Chinese tallow invasion on a longer time (10–20 years) time-scale. This approach would involve promoting the regeneration of fast growing native tree species through effective

control of Chinese tallow during the stand initiation stage (Oliver and Larson, 1996) while establishing and maintaining canopy dominance of native tree species by utilizing their late growth advantage over Chinese tallow. Additionally, site preparation and artificial regeneration of fast growing native species following timber harvest or natural disturbance (e.g., hurricane) could lower invasion risk by Chinese tallow (Gan et al., 2009, Wang et al., 2014) and prevent it from becoming a significant component of the forest canopy. Particularly, managers would need to minimize subsequent Chinese tallow regeneration for at least five years following initial treatments due to a viable and persistent seed bank (Cameron et al., 2000) and vigorous sprouting ability following top-kill (Enloe et al., 2015, Pile et al., 2017d). Specifically, during stand initiation, release treatments, eliminating Chinese tallow and other competing vegetation around desirable native species may help to increase the growth of initially slower growing native species. Once the

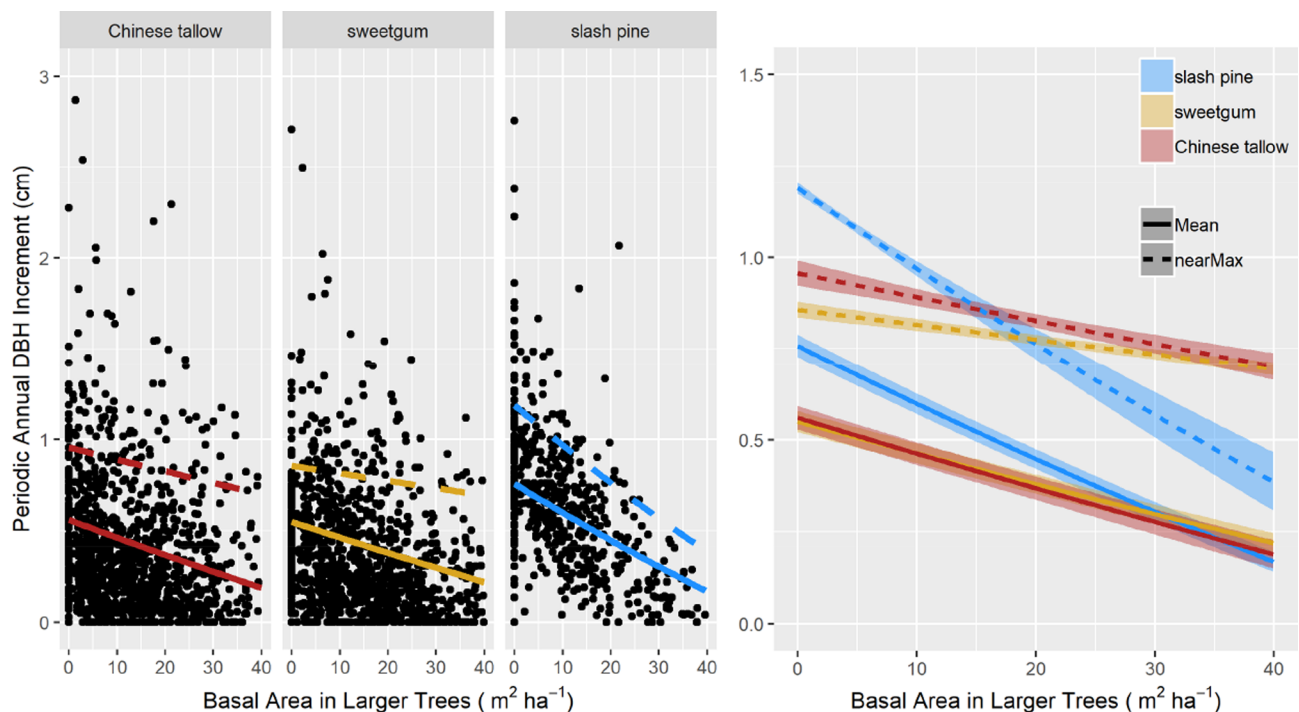


Fig. 10. Periodic annual DBH increment along a competition gradient for Chinese tallow (red), slash pine (green) and sweetgum (yellow) across 1,407 FIA plot records from 6 southern US states. Solid lines depict mean annual increment; broken lines depict near-max (90th percentile) annual increment; ribbon width corresponds to 95% confidence interval for each estimate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stand has reached canopy closure, treatments such as ‘crop tree release’ of desirable species from direct competition with Chinese tallow may favor native tree growth. Further, promoting a well-developed ground vegetation layer including native grasses and shrubs may further limit Chinese tallow establishment (Fan, 2018).

The success of the proposed management approach rests on regenerating native trees that will eventually outcompete Chinese tallow. Although further experimentation is required, based on our findings at both the site and landscape scale, management intervention should occur soon after timber harvest or natural disturbance before Chinese tallow is able to capitalize on its growth advantages under intense competition. Furthermore, we suggest monitoring the effectiveness of those management interventions in controlling Chinese tallow and promoting native species regeneration for at least eight years. Selecting appropriate native tree species with faster early growth rates, taller maximum heights and greater longevity is also key to the success of our suggested approach. For those sites that are used for plantation management, genetically improved growing stock with superior growth rates (e.g., southern pines) may be a good choice for native species.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.05.005>.

References

- Bechtold, W.A., Patterson, P.L. (Eds.), 2005. The Enhanced Forest Inventory and Analysis Program-National Sampling Design and Estimation Procedures. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, Asheville, NC.
- Begon, M., Harper, J.L., Townsend, C.R., 1996. Ecology: Individuals, Populations and Communities, third ed. Blackwell Science, Oxford, Great Britain.
- Bormann, F.H., 1953. Factors determining the role of loblolly pine and sweetgum in early old-field succession in the piedmont of North Carolina. Ecol. Monogr. 23, 339–358. <https://doi.org/10.2307/1948624>.
- Cade, B.S., Guo, Q., 2000. Estimating effects of constraints on plant performance with regression quantiles. Oikos 91, 245–254. <https://doi.org/10.1034/j.1600-0706.2000.910205.x>.
- Cade, B.S., Terrell, J.W., Schroeder, R.L., 1999. Estimating effects of limiting factors with regression quantiles. Ecology 80, 311–323. [https://doi.org/10.1890/0012-9658\(1999\)080\[0311:EEOLFW\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0311:EEOLFW]2.0.CO;2).
- Call, L.J., Nilsen, E.T., 2003. Analysis of spatial patterns and spatial association between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). Am. Midl. Nat. 150, 1–14. [https://doi.org/10.1674/0003-0031\(2003\)150\[0001:AOSPAS\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2003)150[0001:AOSPAS]2.0.CO;2).
- Camarillo, S.A., Stovall, J.P., Sunda, C.J., 2015. The impact of Chinese tallow (*Triadica sebifera*) on stand dynamics in bottomland hardwood forests. Forest Ecol. Manage. 344, 10–19. <https://doi.org/10.1016/j.foreco.2015.02.013>.
- Cameron, G.N., Glumac, E.G., Eshelman, B.D., 2000. Germination and dormancy in seeds of *Sapium sebiferum* (Chinese tallow tree). J. Coastal Res. 16, 391–395.
- Chen, L.Y., Tiu, C.J., Peng, S.L., Siemann, E., 2013. Conspecific plasticity and invasion: invasive populations of Chinese Tallow (*Triadica sebifera*) have performance advantage over native populations only in low soil salinity. Plos One 8. <https://doi.org/10.1371/journal.pone.0074961>.
- Cunard, C., Lee, T.D., 2009. Is patience a virtue? Succession, light, and the death of invasive glossy buckthorn (*Frangula alnus*). Biological Invasions 11 (3), 577–586. <https://doi.org/10.1007/s10530-008-9272-8>.
- D'Antonio, C., Flory, S.L., 2017. Long-term dynamics and impacts of plant invasions. J.

- Ecol. 105, 1459–1461. <https://doi.org/10.1111/1365-2745.12879>.
- Daniels, R.F., 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. *Forest Sci.* 22, 454–456. <https://doi.org/10.1093/forestscience/22.4.454>.
- Dillenburg, L.R., Whigham, D.F., Teramura, A.H., Forseth, I.N., 1993. Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. *Oecologia* 93, 48–54. <https://doi.org/10.1007/bf00321190>.
- Enloe, S.F., Loewenstein, N.J., Streett, D., Lauer, D.K., 2015. Herbicide treatment and application method influence root sprouting in Chinese tallowtree (*Triadica sebifera*). *Invas. Plant Sci. Manage.* 8, 160–168. <https://doi.org/10.1614/IPSMD-14-00062.1>.
- Epa, U.S., 2013. *Level III and IV Ecoregions of the Continental United States*.
- Fan, Z., 2018. Spatial analyses of invasion patterns of Chinese Tallow (*Triadica sebifera*) in a wet slash pine (*Pinus elliottii*) flatwood in the Coastal Plain of Mississippi, USA. *Forest Sci.* 64, 555–563. <https://doi.org/10.1093/forsci/fxy014>.
- Fan, Z., Tan, Y., Crosby, M.K., 2012. Factors associated with the spread of Chinese Tallow in East Texas forestlands. *Open J. Ecol.* 2, 121–130. <https://doi.org/10.4236/oje.2012.23015>.
- Gan, J., Miller, J.H., Wang, H., Taylor, J.W., 2009. Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation. *Can. J. Forest Res.* 39, 1346–1356. <https://doi.org/10.1139/X09-058>.
- Harcombe, P.A., Leipzig, L.E.M., Elisk, I.S., 2009. Effects of hurricane Rita on three long-term forest study plots in east Texas, USA. *Wetlands* 29, 88–100. <https://doi.org/10.1672/08-64.1>.
- Hibbs, D.E., 1983. Forty years of forest succession in central New England. *Ecology* 64, 1394–1401. <https://doi.org/10.2307/1937493>.
- Hirsch, H., Richardson, D.M., Le Reux, J., 2017. Tree invasions: towards a better understanding of their evolutionary dynamics. *AoB Plants*. <https://doi.org/10.1093/aobpla/plx014>.
- Holbrook, N.M., Putz, F.E., 1989. Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (sweet gum). *Am. J. Botany* 76, 1740–1749. <https://doi.org/10.1002/j.1537-2197.1989.tb15164.x>.
- Iponga, D.M., Milton, S.J., Richardson, D.M., 2008. Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South African savanna. *J. Arid Environ.* 72, 612–623. <https://doi.org/10.1016/j.jaridenv.2007.10.001>.
- Johns, D.T., Williams, B., Williams, H.M., Stroupe, M., 1999. Seedling survival and natural regeneration for a bottomland hardwood planting on sites differing in site preparation. In: 10th Biennial Southern Silvicultural Research Conference, USDA For. Serv., Gen. Tech. Rep. SRS-30, Southern Research Station, Asheville, NC, pp. 145–150.
- Jones, R.H., McLeod, K.W., 1990. Growth and photosynthetic responses to a range of light environments in Chinese tallowtree and Carolina ash seedlings. *Forest Sci.* 36, 851–862.
- Kirkman, L.K., Brown, C.L., Leopold, D.J., 2007. *Native Trees of the Southeast: An Identification Guide*. Timber Press Inc, Portland, Oregon.
- Kormanick, P.P., 1990. *Liquidambar styraciflua* L. sweetgum. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North America*. USDA Forest Service, Washington, DC.
- Lin, J., Harcombe, P.A., Fulton, M.R., Hall, R.W., 2004. Sapling growth and survivorship as affected by light and flooding in a river floodplain forest of southeast Texas. *Oecologia* 139, 399–407. <https://doi.org/10.1007/s00442-004-1522-6>.
- Lohrey, R.E., Kossuth, S.V., 1990. *Pinus elliottii* Englem. slash pine. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North America*. USDA Forest Service, Washington, DC, pp. 338–347.
- Marks, P.L., 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.* 44, 73–88. <https://doi.org/10.2307/1942319>.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1).
- Meiners, S.J., Pickett, S.T.A., Cadenasso, M.L., 2002. Exotic plant invasions over 40 years of old field successions: community patterns and associations. *Ecography* 25, 215–223. <https://doi.org/10.1034/j.1600-0587.2002.250209.x>.
- Oliver, C.D., 1978. Development of Northern Red Oak in Mixed Species Stands in Central. Yale University School of Forestry and Environmental Studies, New England.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. Update Edition edition. John Wiley & Sons Inc, New York, NY.
- Oswalt, S.N., 2010. Chinese tallow (*Triadica sebifera* (L.) Small) population expansion in Louisiana, East Texas, and Mississippi. *Res. Note SRS-20*. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, pp. 5.
- Paudel, S., Battaglia, L.L., 2015. The role of light, soil and human factors on the probability of occurrence of an invasive and three native plant species in coastal transitions of coastal Mississippi, USA. *J. Plant Ecol.* 8, 491–500. <https://doi.org/10.1093/jpe/rtu045>.
- Pile, L.S., Wang, G.G., Knapp, B.O., Liu, G., Yu, D., 2017a. Comparing morphology and physiology of southeastern US *Pinus* seedlings: implications for adaptation to surface fire regimes. *Ann. Forest Sci.* 74, 68. <https://doi.org/10.1007/s13595-017-0666-6>.
- Pile, L.S., Wang, G.G., Knapp, B.O., Walker, J.L., Stambaugh, M.C., 2017b. Chinese tallow (*Triadica sebifera*) invasion in maritime forests: the role of anthropogenic disturbance and its management implication. *Forest Ecol. Manage.* 398, 10–24. <https://doi.org/10.1016/j.foreco.2011.06.047>.
- Pile, L.S., Wang, G.G., Stovall, J.P., Siemann, E., Wheeler, G.S., Gabler, C.A., 2017c. Mechanisms of Chinese tallow (*Triadica sebifera*) invasion and their management implications – a review. *Forest Ecol. Manage.* 404, 1–13. <https://doi.org/10.1016/j.foreco.2017.08.023>.
- Pile, L.S., Wang, G.G., Waldrop, T.A., Walker, J.L., Bridges, W.C., Layton, P.A., 2017d. Managing an established tree invader: developing control methods for Chinese tallow (*Triadica sebifera*) in maritime forests. *J. Forest.* 115, 522–529. <https://doi.org/10.5849/JOF-2016-022R2>.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects Models in S and S-PLUS*. Springer-Verlag New York Inc., New York, NY.
- Pyšek, P., Richardson, D.M., 2007. Traits associated with invasiveness in alien plants: where do we stand? *Biol. Invas.* 193, 97–125. https://doi.org/10.1007/978-3-540-36920-2_7.
- R Core Team, 2018. *R: A Language Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rebbeck, J., Hutchinson, T., Iverson, L., Yaussy, D., Fox, T., 2017. Distribution and demography of *Ailanthus altissima* in an oak forest landscape managed with timber harvesting and prescribed fire. *Forest Ecol. Manage.* 401, 233–241. <https://doi.org/10.1016/j.foreco.2017.06.050>.
- Rejmánek, M., Robinson, G.R., Rejmánková, E., 1989. Weed-crop competition: experimental designs and models for data analysis. *Weed Sci.* 37, 276–284. <https://doi.org/10.1017/S0043174500071903>.
- Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J., Pigliucci, M., 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecol. Lett.* 9, 981–993. <https://doi.org/10.1111/j.1461-0248.2006.00950.x>.
- Richardson, D.M., Hui, C., Nuñez, M.A., Pauchard, A., 2014. Tree invasions: patterns, processes, challenges and opportunities. *Biol. Invas.* 16, 473–481.
- Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species – a global review. *Divers. Distrib.* 17, 788–809. <https://doi.org/10.1111/j.1472-4642.2011.00782.x>.
- Scheld, H.W., Cowles, J.R., 1981. Woody biomass potential of the Chinese tallow tree. *Econ. Botany* 35, 391–397.
- Schwinnig, S., 1996. Decomposition analysis of competitive symmetry and size structure dynamics. *Ann. Botany* 77, 47–58. <https://doi.org/10.1006/anbo.1996.0006>.
- Shoulders, E., Tiarks, A.E., 1980. Predicting height and relative performance of major southern pines from rainfall, slope, and available soil moisture. *Forest Sci.* 26, 437–447. <https://doi.org/10.1093/forestscience/26.3.437>.
- Siemann, E., Carrillo, J.A., Gabler, C.A., Zipp, R., Rogers, W.E., 2009. Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. *Forest Ecol. Manage.* 258, 546–553. <https://doi.org/10.1016/j.foreco.2009.03.056>.
- Simberloff, D., Claudi, R., Hendrickson, O., Ottens, H., 2002. Managing established populations of introduced species. In: *Alien Invasive Species: A Threat to Canadian Biodiversity*. Natural Resources Canada, Canadian Forest Service, Ottawa, Canada, pp. 269–278.
- Sun, Y., Gao, H., Li, F., 2017. Using linear mixed-effects models with quantile regression to simulate the crown profile of planted *Pinus sylvestris* var. *mongolica* Trees. *Forests* 8, 446. <https://doi.org/10.3390/f8110446>.
- Tian, N., Fan, Z., Matney, T.G., Schultz, E.B., 2017. Growth and stem profiles of invasive *Triadica sebifera* in the Mississippi coast of the United States. *Forest Sci.* <https://doi.org/10.5849/FS-2016-017R3>.
- Von Holle, B., Motzkin, G., 2007. Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. *Biol. Conserv.* 136, 33–43.
- Wang, G.G., 2003. Early regeneration and growth dynamics of *Populus tremuloides* suckers in relation to fire severity. *Can. J. Forest Res.* 33, 1998–2006. <https://doi.org/10.1139/x03-123>.
- Wang, H.-H., Buchhorn, J.L., Grant, W.E., 2014. Effects of management on range expansion by Chinese Tallow in the forestlands of eastern Texas. *J. Forestry* 112, 346–353.
- Weber, E., 2003. *Invasive Plant Species of the World: A Reference Guide to Environmental Weeds*. CAB International Publishing, Wallington.
- Weiskittel, A.R., Hann, D.W., Kershaw Jr., J.A., Vanclay, J.K., 2011. *Forest Growth and Yield Modeling*. Wiley-Blackwell, West Sussex, UK.
- Zou, J., Rogers, W.E., Siemann, E., 2009. Plasticity of *Sapindus sebiferum* seedling growth to light and water resources: inter- and intraspecific comparisons. *Basic Appl. Ecol.* 10, 79–88.